DIVERSIFICATION OF THE SOUTH AMERICAN AVIFAUNA: PATTERNS AND IMPLICATIONS FOR CONSERVATION IN THE ANDES[1]

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Abstract

By combining distributions and phylogenies for large groups of birds, it is now possible to disentangle the relative roles of contemporary ecology and history in explaining the distribution of biodiversity on earth. In South America, avian lineages, which represent radiations during the warm parts of the Tertiary, are best represented in the tropical lowlands and Andean forelands. During the upper Tertiary, diversification was most intense in the tropical Andes region, with recruitment back into the tropical lowlands and into South America's open biomes. Within the tropical Andes, endemism (mean inverse range size) and mean branch length (number of phylogenetic nodes on lineages) increase from the foothills up to the tree line and then decline again in the barren highlands, suggesting that the tree-line zone plays a special role in the diversification process. The resulting endemism is locally aggregated, often with marked peaks in areas immediately adjacent to ancient population centers. Thus, the process of evolution of new species is linked with local factors that, over a shorter time perspective, were also favorable for people. If we want to maintain the process of diversification, it becomes essential to supplement the traditional approach of preserving biodiversity in wilderness areas with few people with efforts to support sustainable development in populated areas.

Key words: Biodiversity, birds, conservation, South America, speciation.

The tropical Andes region is recognized as one of the principal global hotspots for biodiversity and conservation. Since the term "hotspot" was first launched (Myers, 1989, 1990), it has become a widely used buzzword, applied indiscriminately on different spatial scales, often combining species richness and endemism, although more critical data analysis reveals that spatial variation in species richness is often not congruent with endemism or with the occurrence of threatened species (Orme et al., 2005). Because different measures of biodiversity are idiosyncratic, we cannot use them blindly as a "currency of biodiversity."

Significant strides have been made to analyze to what extent the geographical variation in biodiversity measures reflects ecology, such as contemporary climate and landscape complexity. Ecological models perform quite well in explaining species richness, but closer examination reveals that the results are driven by the many data points representing widespread species, and that the models do not explain local aggregates of species with small distributions, which may instead reflect speciation history (Jetz et al., 2004; Rahbek et al., 2006). With the rapid increase in DNA-based phylogenies, it is now possible to begin to link together the macroecological and historical approaches to biogeography (Fjeldså & Rahbek, 2006; Hawkins et al., 2006; Fjeldså et al., 2007b).

In this paper, we will illustrate how one can analyze large amounts of phylogenetic and distributional data to describe historical components of biodiversity patterns. We will also discuss the relative roles of past history and present ecology in explaining the Andean biodiversity hotspot. To place the Andes in a regional context, we will first take a continent-wide overview and then scale down to examine the hot points within the Andean hotspot. Based on interpretations of distinctive patterns of endemism in the Andes, we will finally discuss where to focus conservation actions.

Materials and Methods

We will base this analysis on bird data. Birds are not perfect indicators of wholesale biodiversity (see

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[1] P. Williams kindly provided the WORLDMAP software to manage the distributional data and to generate Figures 1–4. The databases were developed over more than 10 years through collaboration with numerous institutions and individuals. In addition to the sources listed in earlier populations, we used online databases at Yale University and University of California, Berkeley, and scrutinized maps by S. Herzog, whom we also thank for his assistance with compiling data on elevational distributions of birds in the Carrasco National Park in Bolivia.

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Moore et al., 2003) but are useful in terms of the quality of the available data. The species-level taxonomy is more or less complete, and for most avian groups there are now relatively detailed molecular phylogenies available. Furthermore, enough is known about species distributions to make fairly realistic distribution maps.

DISTRIBUTIONAL DATA

We used two databases of South American bird distributions digitized in the WORLDMAP software (Williams, 1998) based on extensive review of museum collections and literature and comprehensive fieldwork by the first author in the Andes region (see primarily Fjeldså & Krabbe, 1990). These databases are (1) a continent-wide database over all resident birds in a geographical grid of 1 × 1 geographical degrees described, e.g., by Fjeldså and Rahbek (1998) and Rahbek et al. (2006); and (2) a database over the tropical Andes region, in a grid of 15 × 15 geographical minutes (see Fjeldså et al., 1999, 2005a). The latter is the most finely resolved data set of its kind for the Andes. Such high resolution can only be obtained in highly structured landscapes, so this database includes only species that breed at elevations higher than 2500 m (at least in some parts of their ranges), plus lowland species representing the 25% of South American birds with the most restricted geographical ranges. This database contains 300,000 in-grid-cell records, of which 87,000 are confirmed present in a grid cell; the rest represents conservative interpolation in which careful scrutiny of topographic maps and satellite images, including Google Earth (<http://earth.google.com/>), suggests that the species should be present between collecting points. The interpolation is mostly used for species that are generally widespread or ubiquitous (and therefore are rarely reported). For species considered to be rare or local, the use of interpolation is restrictive.

For each grid cell, species richness is defined as the number of species (as accepted by the American Ornithologists' Union) and endemism is defined as range-size rarity, which is the inverse range size (number of grid cells in the species' range). This can be expressed as a mean value per species represented in a cell (mean endemism) or as a sum of inverse range-size scores.

To illustrate variation at the local scale, we used bird data from the Yungas of Cochabamba, Bolivia. It is a local hot point at 16°S, where the species richness is almost as high as near the equator (98.5% compared with the average of four grid cells representing humid Andean slopes adjacent to the equator). The data are based on several ornithological surveys taken between 1991 and 2000 along three elevational transects in the Carrasco National Park (western, central, and eastern parts), from the lowlands over the top ridge of the Tunari Range at ca. 4000 m and into the adjacent rain shadow in the Cochabamba Basin. Because of undersampling in coca-growing areas in the foothills and in some very steep areas at mid-elevation, we found it appropriate to use interpolation to connect species records at different elevations along transects. We also added a few species based on historical records (mainly of widespread but rare species). In addition to the variation in species richness, we examined the variation in range-size rarity (endemism), as calculated from the continent-wide database.

HISTORICAL DATA

The study of avian evolution by Sibley and Ahlquist (1990) has, despite serious problems with their method of molecular phenetics based on DNA-DNA hybridization, already served as a basis for describing the general pattern of accumulation of ancient taxa in the tropical lowland rainforests and more recent diversification in montane areas near the equator and at high latitudes (Fjeldså, 1995; Hawkins et al., 2006).

Today, better data based on DNA sequences are available. We obtained phylogenetic data by literature review and through research collaboration, primarily between the institutions of the two authors, where we aim to generate global molecular phylogenies for the largest avian radiation, the passerine birds (order Passeriformes). We will present geographical distribution patterns for some clades defined through molecular phylogenetic studies, including the historical diversification of the suboscine family Furnariidae (Fjeldså et al., 2005b, 2007b; Irestedt et al., 2006, unpublished data). This family was chosen as an example because it is endemic and diverse (302 species) and has adapted to all terrestrial environments in the continent and is a prominent component of the avifauna of even the harshest environments (Remsen, 2003). Only 60% of the furnariid species have so far been included in molecular phylogenies, but the deeper branches are well resolved, and the sampling gaps in the terminal parts of the phylogeny can therefore be reasonably filled using published judgments about relationships within these subgroups. In some terminal branches with many closely related species, which are left unresolved, branch lengths were assigned to each species by assuming a regular spacing of nodes (thus, a trichotomy translates into 1.6 steps: four species in a clade represent two steps; eight species, three steps; 16 species, four steps, etc.).

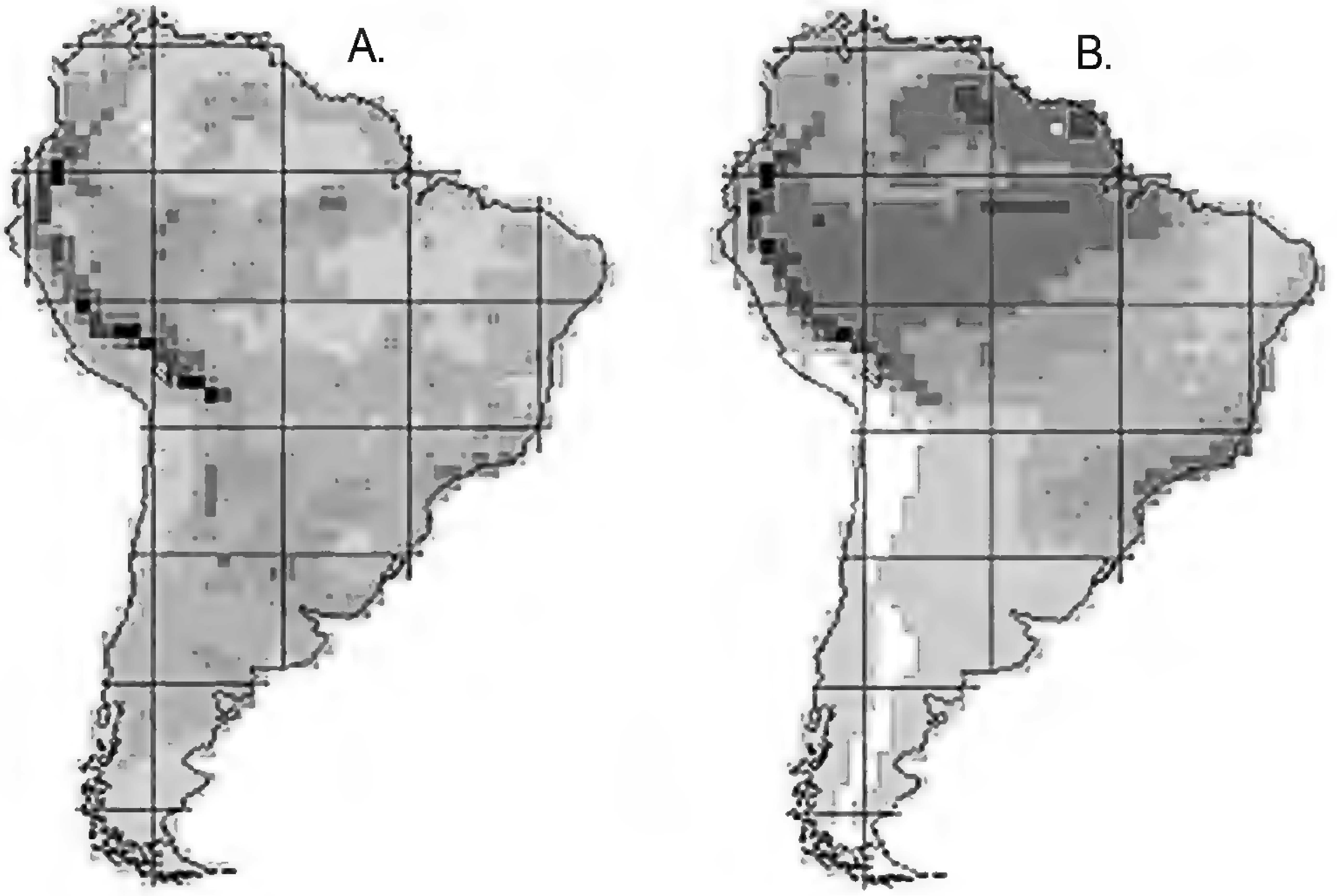

Figure 1. Species richness patterns for ancient avian groups in South America. —A. Sixty-five species representing small avian clades (of one to four species) dating back to the Eocene or before (as judged from molecular evidence). —B. The deep branches of New World flycatchers, altogether 248 species representing Cotingidae, Pipridae, Tityrinae, pipromorphines, and some small clades, all of which had their origin in the Oligocene (Ohlson et al., 2008). Species richness is represented from greatest (black cells) to least (white cells).

Because a chronogram with local calibration points is not yet published for the Furnariidae family, we analyzed the diversification of the group by giving each species a branch-length score, which is the number of nodes to the root of the phylogeny. For a simple illustration, we divided the species into quartiles of branch lengths, with the first quartile being the 25% of the species representing the fewest apparent splitting events since the origin of the group and the fourth quartile being the 25% of the species representing the most splitting events.

RESULTS

VARIATION IN SPECIES RICHNESS IN SPACE AND TIME

By reviewing the published molecular evidence of avian evolutionary relationships, we identified 65 species representing small clades (of one to four species) dating back to the Eocene or even earlier (e.g., rheas, Rheidae; screamers, Anhimidae; hoazin, *Opisthocomus hoazin*; broad-billed Sapayoa, *Sapayoa aenigma*). These species represent lineages in which there was little or no subsequent speciation, or where such events had been erased by extinction (Ricklefs, 2003); we see them here as surviving representatives of the endemic South American avifauna of the Early Tertiary climatic maximum. As illustrated in Figure 1A, these species are today mainly found in the tropics outside the Andes, and to some extent in the subtropics, with peak concentrations in dynamic floodplains with mosaics of swampy and savanna habitats (Sucumbíos/Napo/Pastaza in Ecuador; Loreto and locally near Pucallpa and Madre de Dios, Peru; Bolivian savannas and adjacent Pantanal; the middle reaches of the Amazon River of Pará and savanna mosaics of Amapá, Brazil; Cuyuni–Mazaruni in Guyana). This richness pattern is almost identical to that of the 25% most widespread South American birds, which was found to be best explained from ecosystem productivity (Rahbek et al., 2006). The only difference is a slightly higher representation of ancient species in the hydrologically unstable Chaco.

Our next examples are from the largest endemic South American avian radiation of suboscine passerine birds (more than 1100 species), which is now subject to detailed phylogenetic study (Irestedt et al., 2002, 2004, 2006; Fjeldså et al., 2007a; Tello & Bates, 2007; Ohlson et al., 2008). The early (Middle Tertiary) suboscine radiations (antbirds and gnatcatchers in the tracheophone radiation and cotingas, manakins, tityrines, and pipromorphines in the New

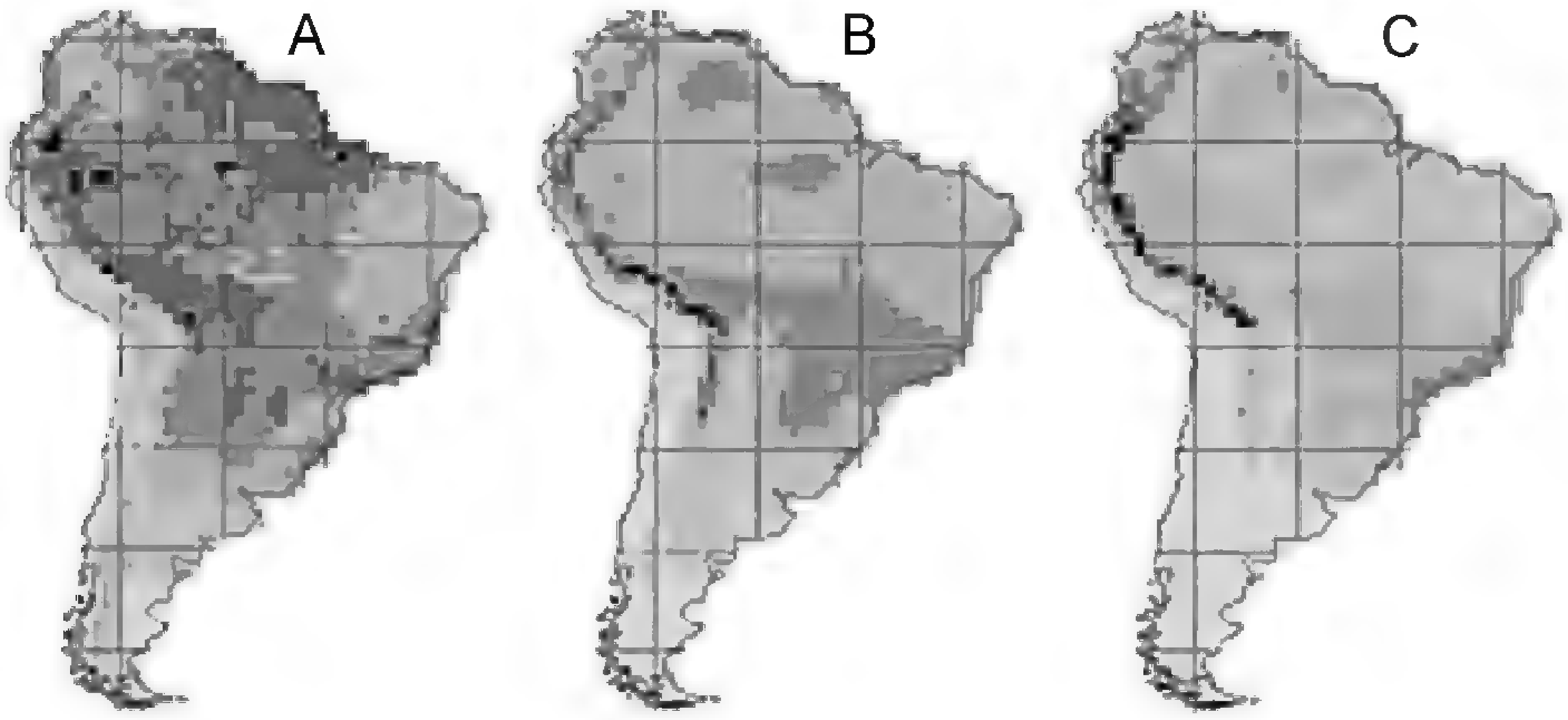

Figure 2. Comparison of species richness patterns for three clades that all diversified after the early Miocene. —A. Core ovenbirds, Furnariinae (Irestedt et al., 2006). —B. New World flycatchers, Tyrannidae (Ohlson et al., 2008). —C. Tanagers, Thraupidae (Jønsson & Fjeldså, 2006). A and B represent ancient South American lineages; C is part of a larger group colonizing from North America. Species richness is represented from greatest (black cells) to least (white cells).

World flycatcher radiation) are all typical groups of the tropical lowland forests. Because a long branch separates the early radiations of New World flycatchers from Neogene radiation (Tyrannidae s. str.) (Ohlson et al., 2008), we present these early flycatcher clades in a map (248 species, Fig. 1B) that illustrates the species richness pattern of a group whose diversification started during the Oligocene and continued to diversify in the same (forest) habitat. The species richness is high throughout the humid tropical forest biomes, with the peak concentration of species in Ecuador and Peru on the transition from the Amazon lowlands toward the Andes.

We illustrate the species richness pattern of groups whose diversification started well into the Miocene, with three species-rich groups as examples; of these, the Furnariinae (core ovenbirds, Fig. 2A) and the Tyrannidae (s. str., Fig. 2B) are subclades of old South American groups, while the tanagers (Thraupidae, Fig. 2C) represent the large group of nine-primaried oscines that colonized from North America. These groups are more broadly distributed than the old groups, including those in the savanna biomes. In particular, all three have their peak concentration in the Andes. The similarity of patterns shows that the intensive radiation of a new taxonomic group in the Andes (Fjeldså & Rahbek, 2006) did not prevent the other two groups from diversifying in this same area. The tropical Andes region stands out clearly as the center of avian diversification during the Neogene.

To illustrate how diversification in an old South American group proceeded up through the Neogene, we subdivide the 302 furnariid species into quartiles of different branch lengths (Fig. 3). The first quartile of species (Fig. 3A), many of them in monotypic genera, represents lineages with low speciation rates or past extinction filters and is mainly found in the forested tropics, notably in upper Amazonian terra firme forest and on the adjacent humid Andean slopes and the northern part of the Andes region, which was more or less isolated by marine transgressions in the early Neogene. The second quartile (Fig. 3B) gives a similar pattern, although with more species associated with areas that once comprised extensive swamp forests, mangroves, and palm savannas fringing marine incursions in the Amazon Basin. The more derived species (third and fourth branch-length quartiles, Fig. 3C, D) are particularly strongly represented in the grassland biomes of the La Plata and Río Negro basins and along the Andes, with the third quartile mainly in the dry-based southern and central Andean highlands and the most terminal branches (fourth quartile) concentrated in the tropical East Andean cloud-forest zone. We also note, in Figure 3D, that there is a certain spillover from the humid Andes to river island habitats along the main Amazonian river channels.

THE ANDEAN HOTSPOT AND ITS LOCAL HOT POINTS

The species richness pattern for range-restricted Andean highland birds (Fig. 4) shows marked hot points within the tropical Andean hotspot. This is less apparent in other studies of avian endemism in the Andes (e.g., Stattersfield et al., 1998), which simply outlined areas characterized by separate sets of species but paid less attention to their strongly aggregated (nested) distribution. Particularly strong aggregates of range-restricted species are found on the humid slopes in southern Chocó (Colombia), near the equator and where the East Andean cloud forest is deeply intersected by valleys (e.g., to either side of the

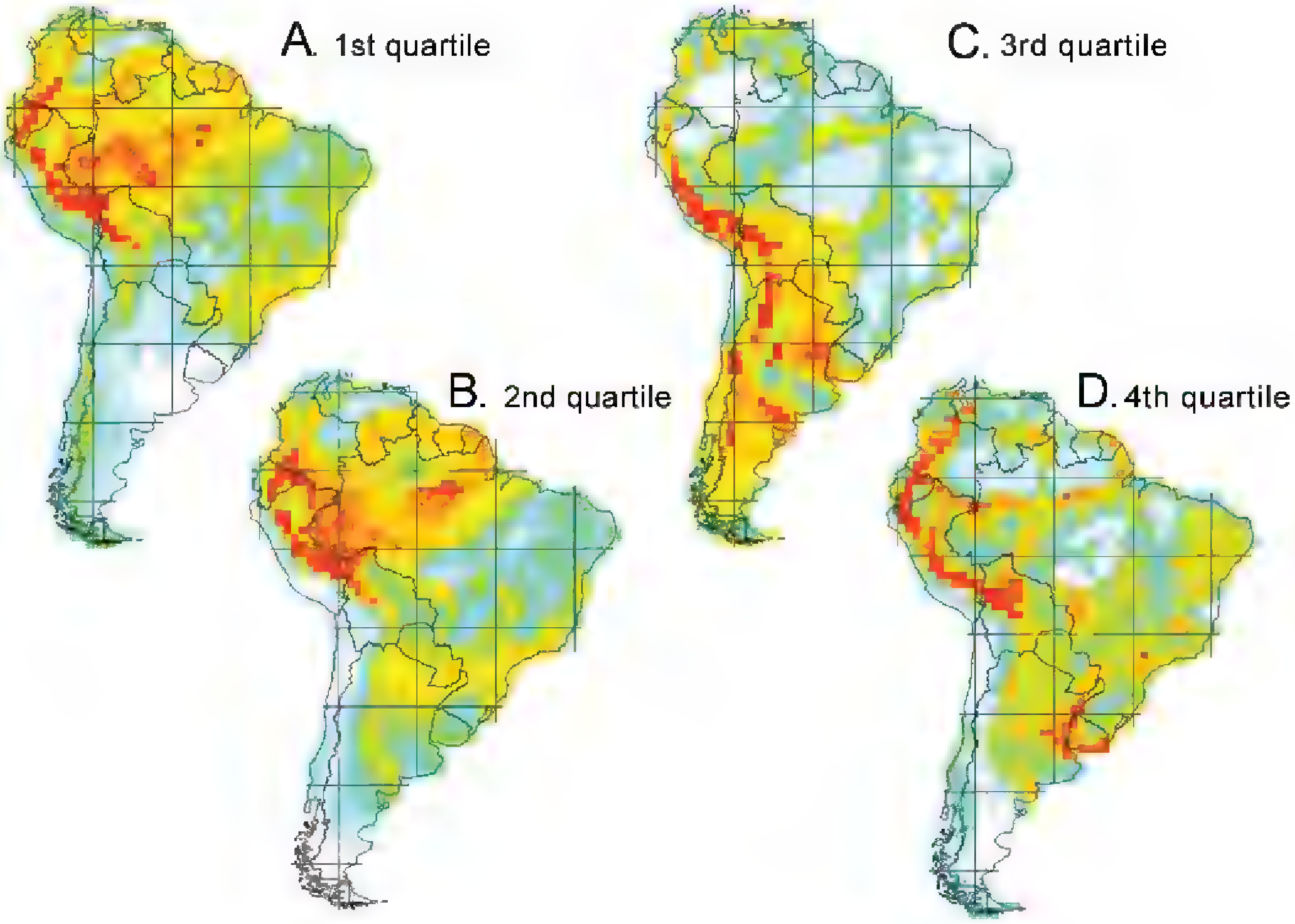

Figure 3. Species richness variation of Furnariidae (ovenbirds and woodcreepers) divided by branch-length quartiles, with the first quartile being the 25% of the species that are the fewest nodes away from the root of the phylogeny and the fourth being the 25% of the species representing the longest (terminal) branches. Red cells represent maximum species richness; white cells represent no species present.

North Peru Low, and in places where the eastern Andean ridge is deeply intersected by valleys in Huánuco and Cuzco [Peru] and southern La Paz [Bolivia]). Fairly high values are also found deeper into the Andes, where distinctive mist zones and cloud forest can be found on the transition between warm valleys and barren highlands (e.g., around the Magdalena Valley, Colombia, on the eastern slope of Cordillera Blanca; in Apurímac–Cuzco, Peru; and around the Cochabamba Basin, Bolivia). Many of the endemic species in these areas are associated with environments near the tree line and with relict patches of high-altitude woodland deeper into the highland.

Typically, the most closely related species inhabit corresponding elevation zones on adjacent slopes (in some cases replacing each other sharply even if there is no obvious barrier), while species replacing each other in different elevation zones on the same slopes (see Krabbe & Schulenberg, 1997) are often more distantly related (review in García-Moreno & Fjeldså, 1999).

THE VARIATION IN AVIAN DIVERSITY ON AN ANDEAN ELEVATIONAL GRADIENT

The local variation in biodiversity parameters within an Andean hot point is illustrated in Figure 5. This elevational transect, from the lowlands up to the ridge of the Cordillera Tunari and over into the rain shadow area in the Cochabamba Basin, has altogether 731 species of birds: 668 recorded on the humid slope and 123 on the slopes of the adjacent rain shadow basin. The species richness curve (full line in Fig. 5) suggests a maximum of 411 species around 500 m elevation and a gradual decline, following a concave curve up through the massively forested midslope to a relative plateau, or shoulder, corresponding to the habitat mosaics around the tree line. From here the species richness drops sharply up to the barren top ridge. In the rain shadow zone, the species richness is lower. The kind of pattern with a diversity peak on the lower slope seems typical of elevation gradients (Rahbek, 1995), although there is some variation between groups in the position of the diversity peak on the slope (Jørgensen & León-Yánez, 1999; Kessler et al., 2001).

The endemism (mean range-size rarity per species, stippled line in Fig. 5) describes a different pattern, with very low levels (widespread species) at the base of the Andes and high levels in the montane forest. The peak is in the tree-line zone, which is at 3400 m in a few places without human impact but is mostly depressed to below 3000 m as a consequence of

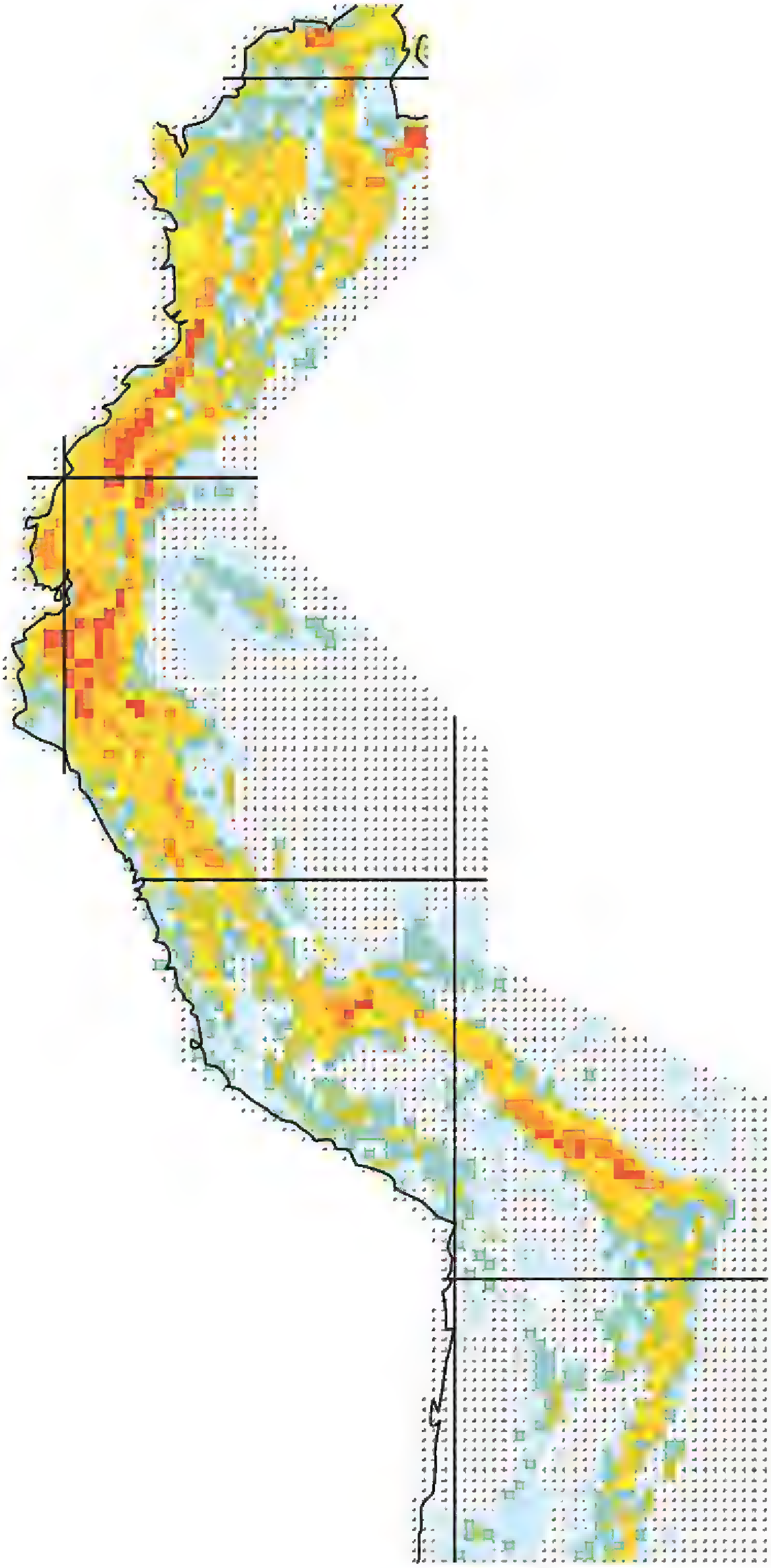

Figure 4. Species richness in the Andes (15′ × 15′ geographical grid) for 470 species representing the lower range-size quartile (25% of species with smallest distributions) of South American birds. Red cells represent maximum species richness; white cells represent no species present.

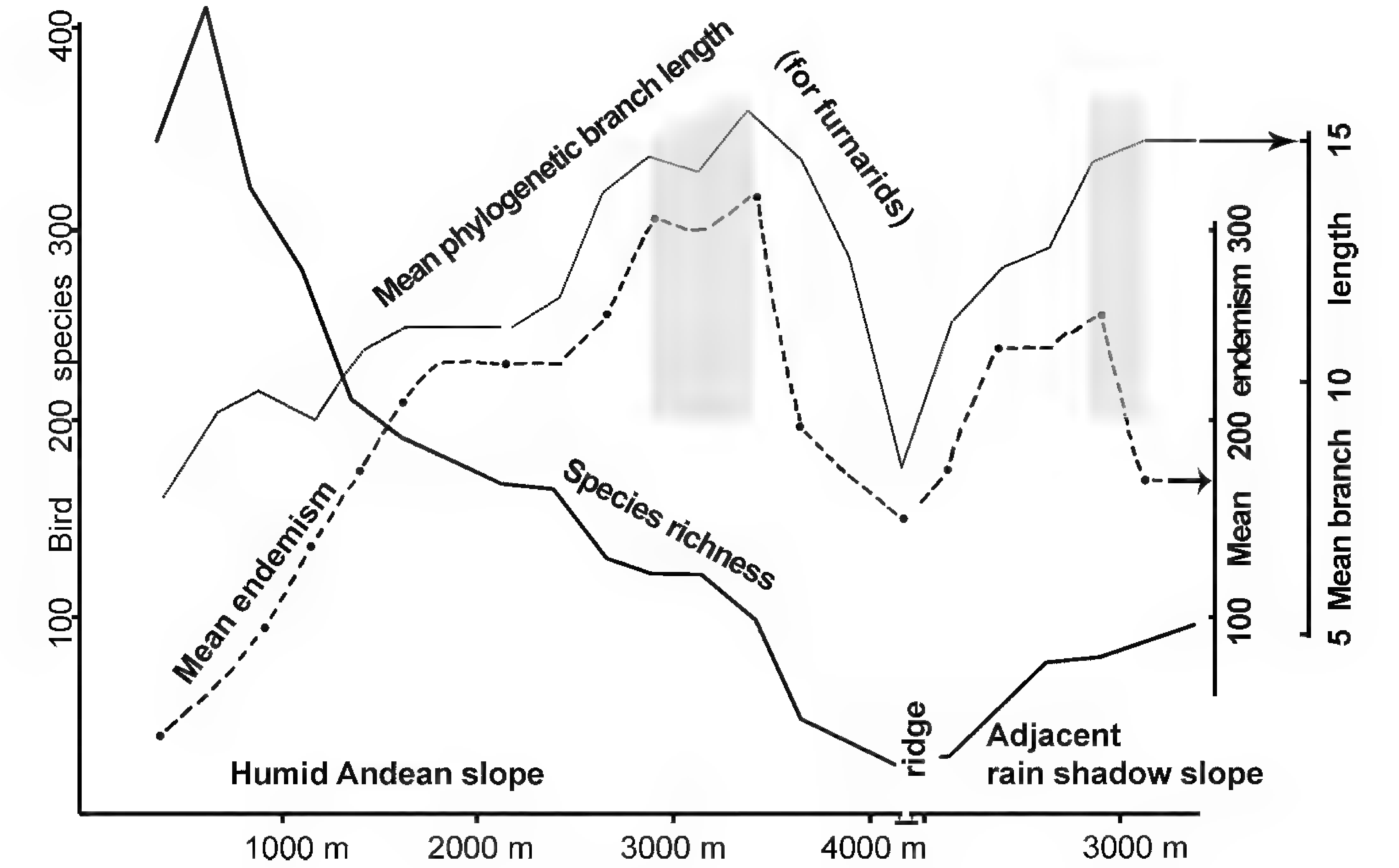

Figure 5. Species richness and endemism along an ecological gradient in the Andes: Carrasco National Park in Bolivia, from lowlands to the highest ridge of Cordillera Tunari and into the adjacent Cochabamba Basin. The tree-line zone, with patchy arboreal vegetation, is shaded. The graph is based on several field surveys between 1991 and 2000 (the first author and local survey results compiled by S. K. Herzog, unpublished data). To compensate for undersampling in coca areas in the foothills and on very steep terrain with difficult access on the midslope, we used interpolations based on historical records from the area and the known elevational limits of species. The index of endemism (stippled curve) is the average inverse range size (number of grid cells in the range of occupancy, as per the 1° distributional database); the branch length (thin line) is the average number of nodes on the phylogenetic branches of the represented furnariid species, based on phylogenies developed by the second author.

incessant burning to create fresh pasture (Kessler & Herzog, 1998). A high mean endemism is also found at 3000–3500 m in the adjacent rain shadow area, where tiny woodland patches can still be found in a highly degraded matrix of bushy habitats and bunchgrass.

To assess whether the high endemism score at the tree line is a simple consequence of the limited areas that are available or reflects a higher rate of speciation, we examined the variation in branch length (number of nodes from the root, for Furnariidae) along the elevational gradient (thin line in Fig. 5). Species representing recent radiations are present both low and high. Nevertheless, the mean branch-length values produce a clear pattern with a predominance of deep branches in the foothills and terminal branches representing more recent radiations in the upper montane forest and on the transition toward the barren highland. Only 54 Furnariidae species were recorded along this gradient, and the sample size is particularly low (five species, with moderately long branches) at the barren top ridge. However, scrutiny of other large taxonomic groups (with good, although not complete, phylogenetic data) suggests that the depicted curve may be fairly typical. Thus, the many range-restricted biological species and sharp spatial replacements (with very few reported cases of hybridization) in the tree-line zone reflect exceptionally high rates of completed speciation in this zone.

DISCUSSION

In agreement with other studies (e.g., Fjeldså, 1995; Hawkins et al., 2006), we found that the tropical lowland rainforest was dominated by species representing basal lineages with a history of little apparent diversification. Paleobotanical evidence suggests that a species richness comparable with contemporary tropical rainforests extended to Patagonia during the Eocene climatic optimum (Wilf et al., 2003), suggesting that the current diversity pattern is a consequence of range contraction and niche conservatism in old clades. Thus, extinction filters (e.g., during the rapid Eocene/Oligocene or Plio-Pleistocene cooling) may explain why these groups are now mainly restricted to the tropics, but lack of opportunities for speciation in featureless lowlands may, of course, also play a role. The densest concentrations of widespread species (Rahbek et al., 2006: fig. 1e) and ancient relictual taxa (Fig. 1A) are found in flat and swampy landscapes, the distribution of which has shifted much in geological time as a consequence of changes in drainage pattern and marine ingressions (Albert et al., 2006) and rapid sedimentation cycles. We must therefore assume that these species persisted by moving around and taking advantage of the patch dynamics and high productivity of the floodplains. Other rainforest groups continued to diversify, but mostly in terra firme forest, and with slow speciation rates overall.

Species with small distributions follow other geographical patterns, with remarkable aggregates in topographically structured parts of the tropics (Orme et al., 2005; Hawkins et al., 2006; Rahbek et al., 2006). Because of a lack of a well-calibrated local molecular clock, our present attempts to link distributions and evolutionary history are imperfect; we still have to use node numbers as a relative measure of recency of speciation. Yet our data provide strong evidence of high rates of speciation in areas of high endemism, both on the large scale (Fig. 3) and on the elevation gradient in the Andes (Fig. 5).

The strong radiation of tanagers (and other colonists from North America) in the Andes did not seem to constrain the rate of radiation on the old endemic South American groups (Fig. 2). Similar patterns of endemism in other well-charted groups (e.g., wild potatoes, Hijmans & Spooner, 2001) support the existence of local centers of intensive speciation in the Andes. Speciation is followed by redistribution and establishment of dense niche packing, for instance on elevation gradients (García-Moreno & Fjeldså, 1999), which means that the ecosystem is accruing more and more species.

Some students of lowland faunas may object to this simple picture and claim that the use of a broad biological species concept in ornithology underestimates the degree of differentiation of the Amazonian avifauna. The variation in mitochondrial DNA of some widespread South American birds suggests distinct evolutionary entities (e.g., Joseph et al., 2001; Lovette, 2004), but it is still unclear to what extent these geographical populations represent species, or whether the results reflect the pattern of sampling or an unusual evolutionary behavior of mitochondrial DNA and the influence of selective sweeps (e.g., Bazin et al., 2006). Admittedly, some widespread lowland species should be split into component phylogenetic species, but a full revision of the South American avifauna would certainly also reveal a need for splitting Andean species. It is unlikely that such a revision would alter the overall pattern.

Intensive speciation in mountains is found only at low latitudes (Rahbek et al., 2006; Hawkins & Diniz-Filho, 2006; Storch et al., 2006; Weir, 2006; Davies et al., 2007). Even at the moderate latitude of 27°N–31°N in the Himalayas, species richness is mainly built up by colonization from outside rather than by local differentiation (Johansson et al., 2007). At high latitudes, similar broad distributions are found in mountainous and flat areas (Hawkins & Diniz-Filho, 2006). Low seasonality in the tropics means reduced seasonal overlap in thermal regimes between low- and high-altitude sites, which is why the individual species could adapt to local conditions (Ghalambor et al., 2006). This leads to dense altitudinal stacking of species (Krabbe & Schulenberg, 1997; García-Moreno & Fjeldså, 1999) and complex patterns of endemism (vicariance, leading to added diversity on coarse-scale geographical analyses; Rahbek & Graves, 2001), in contrast to the wide distributions on high latitudes—even for highland birds (Weir, 2006).

A pertinent question now is whether speciation in the Andes (or other tropical mountains; Fjeldså et al., 2007b) is (1) a specific Plio-Pleistocene phenomenon or (2) a general tendency for diversification to start in topographically structured landscapes but being followed by redistribution as climate-driven range dynamics gradually push the species diversity toward the lowlands, leading to the general correlation with available energy, water, and area (Storch et al., 2006). Figure 3D seems to indicate a spread of furnariids from the Andes along the Amazon (see García-Moreno et al., 1999, for a case of an Andean radiation leading to colonization of Amazonian river island habitats). Similarly, the large radiation of *Tangara* Brisson in South American rainforests started in the Andes (Burns & Naoki, 2004). The furnariid genus *Cinclodes* G. R. Gray, which radiated in the barren Andean highlands, gave rise to two independent colonizations (with speciation) of coastal habitats (Chesser, 2004). Yet, the evidence for montane areas acting as species pumps is still scant, and well-resolved phylogenies of species-rich groups are needed to fully evaluate this interpretation.

FACTORS DRIVING THE DIVERSIFICATION PROCESS

Traditionally, speciation in the Andes has been explained as vicariance (involving observed or hypothesized past barriers; e.g., Vuilleumier, 1980; Jørgensen et al., 1995). Weir (2006) suggests that the intense Pleistocene speciation in tropical mountains could be a result of the marked dispersal barriers created by glaciers and severe elevation shifts of montane vegetation zones in connection with Pleistocene glacial cycles. Weir's analysis may have been biased by the fact that most of the molecular phylogenies he used covered species-rich genera, and he overlooked the fact that many birds of the barren puna are widespread and represent small or even monotypic genera, suggesting that the range dynamics caused by glacial cycles may erase historical population structure rather than promote differentiation (see Jansson & Dynesius, 2002).

Figure 5 suggests that the highest incidence of speciation was around the tree line. Graves (1985, 1988) documented that the highest degree of population differentiation in birds was at the tree line, and he linked this with the high risks of random extinction of local populations within this very narrow habitat band. It should be emphasized here that the tree-line zone is mostly 1 km wide but extends along more than 4000 km. We may not need glaciers to break up the populations of birds in such a habitat band. General environmental instability is enough to lead to relict distributions of some lineages, and thus inevitable divergence of remnant populations by genetic drift.

To understand the mechanisms of speciation, we should perhaps focus less on physical barriers and more on local conditions that allow local source populations to persist despite global climate instability. This could, in turn, allow the development of complex and co-adapted biological communities in places with a benign local climate (as opposed to highlands, where communities change incessantly as a consequence of range dynamics caused by climate change). Fjeldså et al. (1999) demonstrated that peak concentrations of endemic birds at the East Andean tree line correlate with low interannual variation in ground-level climatic conditions, as documented by long series of satellite images. Unfortunately, remotely sensed data of montane habitats are difficult to analyze, and climate models (based on interpolation of data from an insufficient network of weather stations) are far too crude to identify special local environments, such as persistent mist zones on the transition between warm valleys and cold high plateaus. A geographical correspondence between peak values of young endemic species and older relictual forms in the Andes (Fjeldså, 1995) provides indirect evidence for linking speciation with local persistence in stable environments. Still, a thorough evaluation must await detailed analysis of historical population structures, but a sufficiently dense sampling is still lacking for Andean birds (see Bowie et al., 2005, for Afromontane birds, however).

In this context it is interesting to note that high levels of endemism in the Andes correspond (with strong statistical support using data from well-sampled sites only) with ancient cultural centers in the Andes (e.g., Tomebamba [Cuenca], Chavín, Ayacucho–Cuzco, Cochabamba) (Fjeldså, 2007). A positive correlation between biodiversity and population is well known at coarse geographical scales (e.g., Cincotta et al., 2000; Balmford et al., 2001; Araújo, 2003; van Rensburg et al., 2004; Luck, 2007), but the Andean study is on a finer scale (15′ × 15′), and it is interesting to note that the biodiversity/population relationship is stronger for pre-Colombian population centers than for present population patterns, which may be more influenced by external drivers.

The simplest explanation would be that special local conditions in some Andean valleys governed geographical patterns of persistence of bird populations as well as patterns of population growth, albeit at different timescales (Fjeldså, 2007). It is possible that the local conditions that stimulated development of rich (and perhaps co-adapted) biological communities (and thus the cladogenetic process, see Jetz et al., 2004; Rahbek et al., 2006) may also have meant crop predictability. This may, in turn, have been a major prerequisite for the transition from hunter-gatherers to resident farming systems, and for the further advancement of agriculture and development of agricultural centers in certain mountain basins, such as Tomebamba, Cochabamba, and the Ayacucho Valley (Fjeldså et al., 1999; Fjeldså, 2007). The distinct altitudinal zonation (with distinct biological assemblies) may also have facilitated the vertical ecology so characteristic of Andean cultures, with specific crops in specific zones.

IMPLICATIONS FOR CONSERVATION

The effort to preserve biodiversity has traditionally focused on the wilderness; in other words, the unspoiled nature as concept (see Fjeldså, 2007). On a coarse spatial scale, the highest biodiversity in South America is found in the rainforests of the sub-Andean zone and on the humid Andean slopes that are relatively unaltered by humans due to their unsuitability for agriculture, grazing, and forestry (Ortiz, 1975; Young & León, 1999). Because the cloud-forest zone is universally accepted by planners to be inappropriate for large-scale colonization, many national parks were established here. Furthermore, the effect of a moderate disturbance by scattered small farms may not be very different from the patch dynamics caused by frequent landslides on these steep slopes. The conservation situation may only be critical in the Andean forelands and foothills, which are subject to intensive exploitation, notably the growing of coca and uncontrolled logging in Peru (Stotz, 1998; Fjeldså et al., 2005a). This zone has the highest alpha diversity, but on the other hand most of the species are widespread and therefore likely to survive despite local habitat loss (Fig. 5).

Our results suggest that a conservation strategy focused on inaccessible tracts of Andean cloud forest will not be enough. If we are to succeed in slowing the loss of biodiversity, we also need actions where people live, in the montane valleys, and in the transition toward the cloud forest, where people graze their cattle. Here, the primary vegetation is almost nonexistent today (at least in Peru and Bolivia) because of a long history of pastoralism and the use of fire to renew pastures (Kessler & Herzog, 1998). Fortunately, many endemic birds persist remarkably well in small remaining woodlands, and range-restricted plants are also to a large extent associated with degraded habitat or small patches of special (azonal) habitat (Kessler, 1999).

Finding the right solutions requires, first, that we understand the processes underlying the observed patterns of biodiversity and human settlement. The idea of speciation through formation of persistent relict populations in stable local environments (as opposed to traditional focus on barriers) has significant implications. Notably this implies deterministic processes and development of functional assemblages of organisms that may, in turn, mold the ecological processes (Daily, 1997). One of the most prominent ecosystem services provided by Andean biodiversity is the water supply from the elfin forests in specific misty places, situated exactly in the zones identified at hotspots for avian diversification. Such elfin forests represent a distinctive sclerophyllic vegetation type, often of complex structure and overloaded with epiphytes that develop on cloud-enshrouded slopes and that have the ability to comb water out of the mist. Once established, such forests affect the surrounding environment and the livelihood for people living in adjacent valleys (e.g., Campos & Calvo, 2000; Becker et al., 2005). During the past 15 years, a rapidly growing research field suggests that increased species richness may enhance ecosystem productivity, drought resistance, and resilience (e.g., Kinzig et al., 2001). Although this evidence is still mostly based on small experimental plots, the perspective seems highly relevant in relation to the management of those parts of the Andean highland, which now appear as overgrazed bunchgrass steppe.

If the correlation between population and biodiversity in the Andes is more than just two independent effects of suitable environmental settings (Luck, 2007) and if functional links exist (biodiversity enhancing livelihood for people), then we have a potential win-win situation for biodiversity conservation and development. However, in order for this to be realized, conservationists, developers, and local communities must come to terms; biologists must provide precise advice about how nature can help people achieve a better life; and politicians must be willing to pay the cost of setting aside essential tracts of land and support innovative development for higher production on some parts of the land (Green et al., 2005).

Unfortunately, the discussion about where to focus conservation efforts is full of rhetoric of little scientific value when organizations focus on funding points (e.g., for the Andean Dispersal Corridor, or before that for the "green lungs" of the Amazon rainforest). In this context, the small pockets of remaining tree-line habitat in the Andes have been rejected as "the living dead" and therefore not worth saving (Ibisch et al., 2005: 84). We have tried to illustrate that these areas are indeed sites of important processes, both with respect to the diversification process and to suitable conditions for people. The promotion of conservation in these areas is outside the scope of our paper but nonetheless will benefit from insights developed from consideration of patterns of biodiversity and their underlying processes.

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